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Resting eggs in free living marine and estuarine copepods

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Marine free living copepods can survive harsh periods and cope with seasonal fluctuations in environmental conditions using resting eggs (embryonic dormancy). Laboratory experiments show that temperature is the common driver for resting egg production. Hence, we hypothesize (i) that seasonal temperature variation, rather than variation in food abundance is the main driver for the occurrence of the resting eggs strategy in marine and estuarine copepod species; and (ii) that the thermal boundaries of the distribution determine where resting eggs are produced and whether they are produced to cope with warm or cold periods. We compile literature information on the occurrence of resting egg production and relate this to spatio-temporal patterns in sea surface temperature and chlorophyll *a* concentration obtained from satellite observations. We find that the production of resting eggs has been reported for 42 species of marine free living copepods. Resting eggs are reported in areas with high seasonal variation in sea surface temperature (median range 11°C). Temporal variation in chlorophyll *a* concentrations, however, seems of less importance. Resting eggs are commonly produced to cope with both warm and cold periods and, depending on the species, they are produced at the upper or lower thermal boundaries of a species' distribution.

KEYWORDS: embryonic dormancy; seasonality; thermal boundaries; chlorophyll; aestivation; overwintering

INTRODUCTION

Organisms living in unstable environments are exposed to adverse conditions of varying length (e.g. unfavourable temperature and food availability) and traits have therefore developed to allow species to cope with this

adversity. It is known that marine calanoid copepods can survive adverse environmental conditions as resting eggs (dormant embryos), and can therefore disappear periodically from the plankton (Dahms, 1995; Marcus, 1996). There is general consensus that there are two

types of resting eggs; quiescent and diapause eggs. Quiescent resting eggs are embryos responding to adverse conditions by going into dormancy. These resting eggs are not related to seasonality, but related to fast and unpredictable changes in living conditions such as oxygen deficiency, abrupt salinity changes and crowding (Ban and Minoda, 1994; Holmstrup *et al.*, 2006; Højgaard *et al.*, 2008). In contrast, the production of diapause eggs is predetermined by the females (Grice and Marcus, 1981; Uye, 1985; Dahms, 1995). These eggs can survive in the sediment for a time that by far exceeds the time scale of the seasonal adverse conditions. Viable diapause eggs from marine copepods have been estimated to be up to 70 years old (Marcus *et al.*, 1994; Madhupratap *et al.*, 1996; Sichlau *et al.*, 2011), and in freshwater even up to several hundred years old (Hairston *et al.*, 1995; Jiang *et al.*, 2012). Compared with a monthly time span for quiescent eggs viability (Drillet *et al.*, 2006), it is therefore expected that the older eggs found in sediment samples are predominantly diapause eggs.

The trigger for the production of resting eggs can be driven by token stimuli (i.e. non-lethal environmental conditions) and is therefore not the underlining reason for their production. If their production is predetermined, however, the characteristics of the environment in which they are found might explain why they are produced. Resting eggs represent a strong link between the pelagic and benthic environments, as the abundance of resting eggs in the sediment is significant, ranging from 10^4 to 10^7 m^{-2} (Marcus, 1989; Næss, 1991; Hairston, 1996; Jiang *et al.*, 2004; Glippa *et al.*, 2011). There is a large variation in the production of resting eggs as some individuals in a population produce varying fractions of eggs as resting eggs, while others do not produce resting eggs at all (Marcus, 1984b; Avery, 2005b; Drillet *et al.*, 2011). Drillet *et al.* (2015) showed that 5–9% of the egg production by a >30 years old laboratory population of *Acartia tonsa* at all times were resting eggs, despite consistently favourable conditions. Avery (2005a) examined the influence of temperature and photoperiod on the production of resting eggs in *Acartia hudsonica* and found temperature to be the primary environmental driver for the production of resting eggs. However, a large variation in the fraction of resting eggs that were produced (42–85%) was ascribed to differences between individuals. Within the same treatments individual production of resting eggs varied from nearly 0 to 100% of the eggs produced. Furthermore, geographically separated populations can differ in their ability to produce resting eggs (Marcus, 1984b; Avery, 2005a; Drillet *et al.*, 2011). Production of resting eggs is clearly influenced by individual variation and population differences, and thus seems a very flexible trait.

For resting eggs to successfully cope with seasonal changes in the environment, the use of cues that signal future changes in environmental conditions may be important. During the winter period, copepods are expected to be exposed to low food availability and low temperature. These two factors are the most characteristic factors that change seasonally. Many copepod species, have been shown to increase the production of resting eggs as a function of temperature and/or photoperiod (Arndt and Schnese, 1986; Dahms, 1995; Chinnery and Williams, 2003; Drillet *et al.*, 2006; Holste and Peck, 2006; Wu *et al.*, 2006; Hansen *et al.*, 2010; Yoshida *et al.*, 2012; Berasategui *et al.*, 2013; Glippa *et al.*, 2013; Peck *et al.*, 2015). However, other abiotic and biotic factors also elicit the production of resting eggs, such as food availability (Drillet *et al.*, 2011), abrupt salinity changes (Højgaard *et al.*, 2008) and crowding (Ban and Minoda, 1994). For instance, it has been observed that reduced food availability can decrease the fraction of resting eggs in the freshwater copepod *Onychodiaptomus birgei* (Walton, 1985). However, the most common cue in marine copepods for inducing the production of resting eggs or breaking their dormancy is temperature (Drillet *et al.*, 2006; Berasategui *et al.*, 2013). Interestingly, resting eggs produced by some copepod species require periods of either warm or cold conditions in order to allow (Sullivan and McManus, 1986) or increase hatching (Uye *et al.*, 1979; Uye, 1985; Næss, 1996; Chen and Marcus, 1997) and some species produce resting eggs primarily at either high or low temperatures (Johnson, 1980; Arndt and Schnese, 1986; Peck *et al.*, 2015). This suggests that these resting eggs are produced to cope with either winter or summer conditions and therefore a strategy related to seasonality. Based on evidence from laboratory studies we hypothesize that (i) seasonal variation in temperature, rather than variation in food availability, is the main driver for the occurrence of resting eggs in marine and estuarine copepod species; (ii) the thermal regime supporting the production of resting eggs, on a species level, depends on the thermal distribution of the species, where resting eggs are produced towards the boundaries of their thermal distribution. We test the hypothesis by comparing reported spatio-temporal occurrences of resting eggs with the seasonal variation in sea surface temperature and chlorophyll *a* concentrations.

METHOD

We used Web of Knowledge, based on predefined search criteria (resting eggs, dormant eggs and embryonic dormancy in combinations with copepods or

species names), to identify studies on resting egg production in marine copepods. Species names are based on the nomenclature of the World Register of Marine Species (WoRMS Editorial Board, 2016). To examine the global distribution of the “resting egg production trait”, we used three different approaches.

First, we compiled all reports of the occurrence of resting eggs in marine sediments where the species had been determined. We also included studies where field collected copepods were shown to produce resting eggs in laboratory incubation immediately following the collection. The location where the copepods originate from was used as the location for the production of resting eggs. If coordinates were not provided for the location where samples of resting eggs or adults had been collected, then published maps and written descriptions were used to determine the spatial reference. We did not distinguish between different types of resting eggs (i.e. diapause or quiescent eggs) but the eggs were categorized according to whether they were produced to cope with warm or cold periods. If the purpose of the production was not explicitly stated in the original articles, they were put into these categories according to how temperature affected hatching patterns and the production of resting eggs and how season affected occurrence and hatching patterns of resting eggs *in situ*.

Secondly, we mapped the global distribution of species that are known to be able to produce resting eggs using presences data from Ocean Biogeography Information System (OBIS, 2016), covering the period from 1902 to 2013. Spatial data for all species producing resting eggs were not available, and therefore *Acartia teclae* and *Sulcanus conflicus* are not included in this analysis.

Finally, we used data from the Continuous Plankton Recorder (CPR) (Richardson *et al.*, 2006) to investigate the relative contribution of the weight fraction of taxa producing resting eggs in copepod assemblages and their spatial distribution in the North Atlantic. We used roughly 49 000 abundance-class observations for 67 copepod taxa in the North Atlantic and adjacent Seas that were made in the period 1998–2008 (Johns, 2014). Distributions of weight fractions were estimated following a two-step approach. Firstly, we determined the weight fraction of resting egg producing taxa for each observed assemblage by weighting their relative abundances with their cubed body length, assuming isomorphism for all copepod taxa (body length data taken from Brun *et al.* (2017)). Secondly, we produced spatial interpolations of the weight fractions across the sampled area using the Integrated Nested Laplace Approximation approach (Rue *et al.*, 2009). Distributions of weight fractions were assumed to be isotropic Gaussian Fields

(Blangiardo and Cameletti, 2015) with beta-binomial error distributions. The interpolation was made using the Stochastic Partial Differential Equation approach and a discrete mesh to approximate the spatial relationships (Appendix 1).

To compare the distribution of species producing resting eggs with the seasonality of the environment, we used data on monthly differences in sea surface temperature ($T_{\max} - T_{\min}$) and chlorophyll *a* concentration ($\text{Chl}_{\max} - \text{Chl}_{\min}$). Data on temperature were extracted from the Hadley Centre (Rayner *et al.*, 2003). We used monthly averages of the HadISST1 product for the period 1981–2010. We estimated seasonal variation in temperature simply by calculating the difference between the annual maximum and minimum temperatures, computed in a 1° latitude-longitude grid. Seasonality in chlorophyll *a* concentration was calculated similarly based on average monthly concentrations (mg m^{-3}) based on merged data extracted from GlobeColour (<http://www.globcolour.info/>) covering the period from 1997 to 2010. Mean values for seasonal variation in temperature and chlorophyll *a* concentrations were calculated within equally sized circles ($\theta = 111$ km) around the points where resting eggs had been registered.

Analyses of the relationship between where resting eggs are produced as a response to low and high temperatures and how this relates to the thermal distribution of the species were conducted on eight selected copepod species. These were exemplified by low temperatures: *Acartia tonsa*, *Eurytemora affinis* and *Labidocera aestiva*; high temperatures: *Acartia hudsonica*, *Centropages abdominalis*, and *Anomalocera patersoni*; high and low temperatures: *Acartia bifilosa* and *Centropages hamatus*. The species were selected based on several criteria: (i) difference in their distribution (global vs. regional); (ii) availability of distribution data; (iii) availability of data for several locations with resting eggs. We used species distribution modelling to estimate the thermal niche of each of these species from their observed distributions. For the period 1960–2013, we matched presence locations and times with corresponding temperature information. From these data, we then estimated habitat suitability in relation to temperature using the MaxEnt species distribution modelling technique (Phillips *et al.*, 2006). For the MaxEnt algorithm we used background temperatures based on approximately 10 000 randomly sampled points that were uniformly distributed in space and time, and disabled threshold features to keep the model fits at a reasonable complexity. Analyses were performed with the MaxEnt software 3.3.3c (<http://www.cs.princeton.edu/~schapire/maxent/>). Similarly, we matched locations where resting eggs have been found in the sediment with temperature data. For species that

produce resting eggs to cope with cold periods, we considered the coldest month, and for species producing resting eggs for warm periods, we considered the warmest month. Sometimes temperature data was not available for the exact location where resting eggs were found, in particular when observations were made very close to the coast. In these cases we assumed temperature to be equal to the temperature of the closest grid cell with information.

STATISTICAL METHODS

All data failed the Shapiro–Wilks test for normality, and a non-parametric Kolmogorov–Smirnov test was therefore applied to test the difference in global seasonal variation in sea surface temperature and chlorophyll *a* concentrations with data from areas where resting eggs were found. All statistical analysis were conducted using GraphPad software version 7.02 (GraphPad Software, La Jolla California USA) with $\alpha = 0.05$. Mean values are reported ± 1 SD.

RESULTS

We found that 42 copepod species belonging to six families (Acartiidae, Centropagidae, Pontellidae, Sulcanidae, Temoridae and Tortanidae) have been reported to produce resting eggs (Table 1). Out of these, 21 species produce resting eggs solely to cope with cold periods, 6 to cope with warm periods and 7 produce resting eggs to overcome both periods with warm and cold conditions. For the last 8 species it has not been possible to determine whether they are produced to cope with cold or warm conditions.

Locations where resting eggs have been found are in temperate areas and mainly on the northern hemisphere between 20 and 70°N, with few additional observations on the southern hemisphere (the Bahía Blanca estuary in Argentina (39°S) and Warrnambool in Australia (38°S)) (Fig. 1). This coincides with the distribution of species that are known to be capable of producing resting eggs, as they are distributed primarily in the temperate regions of the North Atlantic, North Indian Ocean and North Pacific Ocean (Fig. 1). Resting eggs were not only found in areas where there are many observations of species that produce resting eggs but also where there are only few records of species producing resting eggs (Fig. 1). Based on the analysis of the importance of species producing resting eggs in the North Atlantic, it shows that these species form the largest fraction of the

copepod assemblages in shelf areas and offshore throughout the mid-Atlantic (Fig. 2).

The average global seasonal variation in chlorophyll *a* was estimated to be $0.6 \pm 1.6 \text{ mg m}^{-3}$. Resting eggs were found in areas where the average seasonal variation in chlorophyll *a* was $3.57 \pm 4.06 \text{ mg m}^{-3}$, hence in regions where the seasonality in chlorophyll *a* was significantly higher than the global chlorophyll *a* range ($P = 0.0025$) (Fig. 3A and B). Similarly, resting eggs were produced in areas where the average seasonal variation in temperature was significantly higher ($11.0 \pm 3.3^\circ\text{C}$) than the global variation ($3.8 \pm 2.8^\circ\text{C}$) ($P < 0.0001$) (Fig. 4A and B). However, more interestingly, 50% of all records of resting eggs are from areas with a seasonal variation in temperature of $>10^\circ\text{C}$, which accounts for only 5% of the global data set. The presence of resting eggs therefore appears to depend on seasonality of temperature, which is also consistent with the temperate distribution of species producing resting eggs (Fig. 1).

Resting eggs produced to cope with either cold or warm periods have a similar spatial distribution (Fig. 5A and B). However, north of 54°N resting eggs are only produced to cope with cold conditions (Fig. 5A). The seasonal variation in temperature in areas where resting eggs are produced to cope with low temperatures is $10.4 \pm 3.4^\circ\text{C}$, and for resting eggs produced to cope with high temperatures it is $9.9 \pm 4.0^\circ\text{C}$. Hence, the seasonal variation in temperature that induces both of these two strategies appears to be similar.

The eight copepod species selected for detailed analyses differ in their global distributions: some are present regionally (*A. bifilosa*, *A. hudsonica*, *A. patersoni*, *E. affinis* and *L. aestiva*) and others are more cosmopolitan (*A. tonsa*, *C. abdominalis* and *C. hamatus*). The analysis showed that resting eggs are found primarily towards the thermal limits of the species' distribution (Fig. 6). Resting eggs to cope with cold conditions are found toward the lower thermal limit and resting eggs used for coping with warm conditions are found towards the upper limit of the species thermal distribution, which is often seen as a latitudinal adaptation. There is, however, one exception: *A. tonsa*, which produces resting eggs throughout its thermal distribution (Fig. 6).

DISCUSSION

Main findings

We show that resting eggs are found in areas with a high seasonal variation in temperature, and it appears that seasonal fluctuations in chlorophyll *a* concentration are of less importance. Resting eggs to cope with cold or

Table I: Copepod species producing resting eggs divided into categories depending on whether the eggs are produced to cope with warm or cold periods

| Category | Species | References |
|--|---|---|
| Resting eggs in response to low temperatures | <i>Acartia (Acanthacartia) californiensis</i> | Johnson (1980)* |
| | <i>Acartia (Acanthacartia) italica</i> | Belmonte (1997)* |
| | <i>Acartia (Acanthacartia) tonsa</i> | Marcus (1984b, 1991)*, Arndt and Schnese (1986)*, Sullivan and McManus (1986)*, Sabatini (1989), Miller and Marcus (1994), Madhupratap <i>et al.</i> (1996)*, Chen and Marcus (1997)*, Katajisto <i>et al.</i> (1998)*, Castro-Longoria (2001)*, Suderman and Marcus (2002), Hoffmeyer <i>et al.</i> (2009)*, Scheef and Marcus (2010), Sichlau <i>et al.</i> (2011), Berasategui <i>et al.</i> (2013)*, Peck <i>et al.</i> (2015)* |
| | <i>Acartia (Acartiura) teclae</i> | Næss (1996)* |
| | <i>Acartia (Hypoacartia) adriatica</i> | Belmonte (1997)* |
| | <i>Acartia (Odontacartia) erythraea</i> | Kasahara <i>et al.</i> (1975)*, Uye <i>et al.</i> (1979)* |
| | <i>Calanopia thompsoni</i> | Kasahara <i>et al.</i> (1975)*, Uye <i>et al.</i> (1979)* |
| | <i>Eurytemora affinis</i> | Johnson (1980), Næss (1991, 1996)*, Marcus <i>et al.</i> (1994), Viitasalo <i>et al.</i> (1994), Viitasalo and Katajisto (1994), Katajisto (1996)*, Madhupratap <i>et al.</i> (1996)*, Katajisto <i>et al.</i> (1998)*, Albertsson and Leonardsson (2001)*, Glippa <i>et al.</i> (2011, 2013)* |
| | <i>Eurytemora pacifica</i> | Solokhina (1992)* |
| | <i>Labidocera aestiva</i> | Grice and Gibson (1975)*, Grice and Lawson (1976)*, Marcus (1979)*; Marcus (1984a,b)* |
| | <i>Labidocera rotunda</i> | Uye <i>et al.</i> (1979)*, Itoh and Aoki (2010)* |
| | <i>Labidocera wollastoni</i> | Grice and Gibson (1982)*, Lindley (1986, 1990)*, Siokou-Frangou <i>et al.</i> (2005) |
| | <i>Paracartia grani</i> | Guerrero and Rodriguez (1998)*, Boyer and Bonnet (2013)*, Boyer <i>et al.</i> (2013)*, Lindeque <i>et al.</i> (2013) |
| | <i>Paracartia latisetosa</i> | Belmonte (1992), Siokou-Frangou <i>et al.</i> (2005), Belmonte and Pati (2007)* |
| | <i>Pontella meadii</i> | Grice and Gibson (1977)*, Chen and Marcus (1997) |
| | <i>Pontella mediterranea</i> | Sazhina (1968)*, Grice and Gibson (1981)*, Santella and Ianora (1990)*, Romano <i>et al.</i> (1996) |
| | <i>Pteriacartia josephinae</i> | Belmonte and Puce (1994)* |
| | <i>Tortanus (Boreotortanus) discaudatus</i> | Marcus (1990, 1995)* |
| | <i>Tortanus (Tortanus) forcipatus</i> | Kasahara <i>et al.</i> (1975)*, Chen and Li (1991), Dahms <i>et al.</i> (2006) |
| | <i>Sulcanus conflictus</i> | Newton and Mitchell (1999)* |
| | <i>Centropages ponticus</i> | Sazhina (1968)* |
| | <i>Acartia (Acartiura) hudsonica</i> | Marcus (1984b), Sullivan and McManus (1986)**, Marcus <i>et al.</i> (1994), Avery (2005a)** |
| | <i>Acartia (Acartiura) omorii</i> | Itoh and Aoki (2010)** |
| | <i>Anomalocera patersoni</i> | Ianora and Santella (1991)** |
| | <i>Centropages abdominalis</i> | Kasahara <i>et al.</i> (1975)**, Uye <i>et al.</i> (1979)**, Itoh and Aoki (2010)** |
| | <i>Eurytemora americana</i> | Marcus (1984b), Berasategui <i>et al.</i> (2012)** |
| | <i>Sinocalanus tenellus</i> | Hada <i>et al.</i> (1986)** |
| Resting eggs in response to high and low temperatures | <i>Acartia (Acanthacartia) bifilosa</i> | Viitasalo (1992)*, Zhong and Xiao (1992), Katajisto (1996)*, Katajisto <i>et al.</i> (1998)*, Castro-Longoria and Williams (1999)**, Chinnery and Williams (2003)*, Uriarte and Villate (2006)** |
| | <i>Acartia (Acanthacartia) steueri</i> | Uye (1980, 1983)*, Onoue <i>et al.</i> (2004)** |
| | <i>Acartia (Acartiura) clausi</i> | Kasahara <i>et al.</i> (1975)**, Uye <i>et al.</i> (1979)***, Uye (1980), Marcus (1990, 1995)***, Næss (1991, 1996)*, Lindeque <i>et al.</i> (2013) |
| | <i>Acartia (Odontacartia) pacifica</i> | Zhong and Xiao (1992), Jiang <i>et al.</i> (2004, 2006)*, Wang <i>et al.</i> (2005a)** |
| | <i>Centropages tenuiremis</i> | Kasahara <i>et al.</i> (1975)*, Uye <i>et al.</i> (1979)***, Wang <i>et al.</i> (2005b)***, Wu <i>et al.</i> (2006)***, Itoh and Aoki (2010)*, Xu <i>et al.</i> (2011) |
| | <i>Centropages hamatus</i> | Pertzova (1974)*, Marcus (1984b, 1989)***, Lindley (1986, 1990)*, Madhupratap <i>et al.</i> (1996), Chen and Marcus (1997)***, Marcus and Lutz (1998)***, Murray and Marcus (2002), Castellani and Lucas (2003), Engel and Hirche (2004)*, Sedlaeck (2008), Sichlau <i>et al.</i> (2011) |
| | <i>Temora longicornis</i> | Lindley (1986, 1990)*, Næss (1996)*, Castellani and Lucas (2003)***, Engel and Hirche (2004), Glippa <i>et al.</i> (2011) |
| | <i>Acartia (Acartiura) discaudata</i> | Lindeque <i>et al.</i> (2013) |
| | <i>Anomalocera ornata</i> | Chen and Marcus (1997) |
| | <i>Centropages velificatus</i> | Chen and Marcus (1997) |
| Unknown | <i>Epilabidocera amphitrites</i> | Johnson (1980), Marcus (1990, 1995) |
| | <i>Labidocera mirabilis</i> | Chen and Marcus (1997) |
| | <i>Labidocera scotti</i> | Chen and Marcus (1997) |
| | <i>Eurytemora velox</i> | Gaudy and Pagano (1987) |
| | <i>Tortanus (Eutortanus) derjugini</i> | Chen and Li (1992) |
| No spatial reference | | |

Asterisks after the references denotes whether the reference was used for categorizing the species to produce resting eggs to cope with low (*) or high (**) temperatures, if nothing is noted, it has not been possible using these studies to categorize the resting eggs. The species names are based on the nomenclature of World Register of Marine Species (WoRMS Editorial Board, 2016).

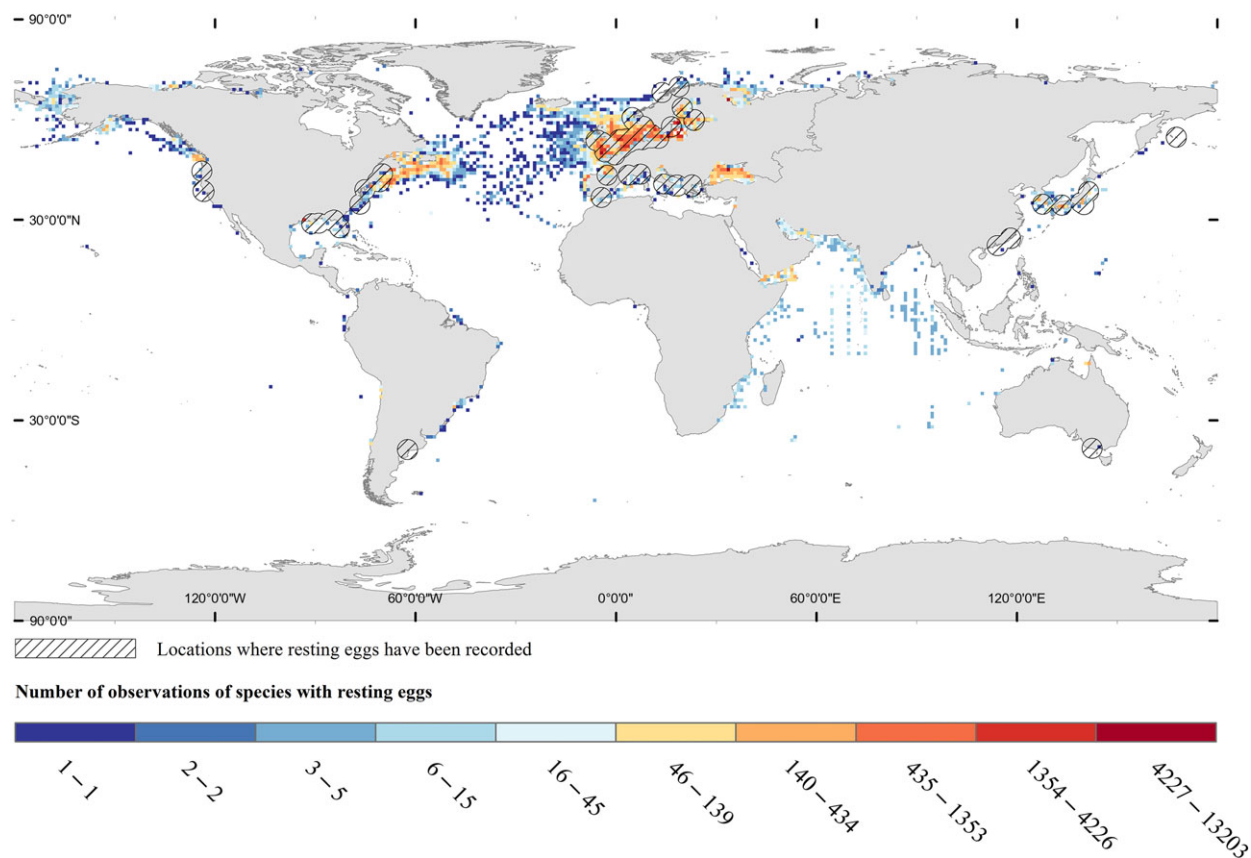


Fig. 1. Distribution of free living marine calanoid copepod species that can produce resting eggs, based on data from OBIS (2016) covering the period from 1902 to 2013 ($n = 207\,067$), and locations where resting eggs have been found. Grid cells in a 1° latitude-longitude grid are coloured according to the number of observations of species known to produce resting eggs within each cell.

warm periods are found in areas with similar seasonal range in temperature and their occurrence overlap, suggesting that their production does not relate to global distribution of the resting egg trait. For several species we find that resting eggs are produced primarily at the species upper and/or lower thermal boundaries of their distribution, suggesting that the signal in the distribution of resting eggs could be related to species' thermal tolerance. Even though resting eggs are found primarily in the neritic environment, species known to produce resting eggs, have relatively high concentration in some off-shore regions.

Which species produce resting eggs?

Here we revise the number of copepod species producing resting eggs previously assessed (Uye, 1985; Marcus, 1989; Mauchline, 1998). The more restricted number reported here is due to several practical and confounding factors: firstly only published original articles have been used in this study, therefore excluding species such as

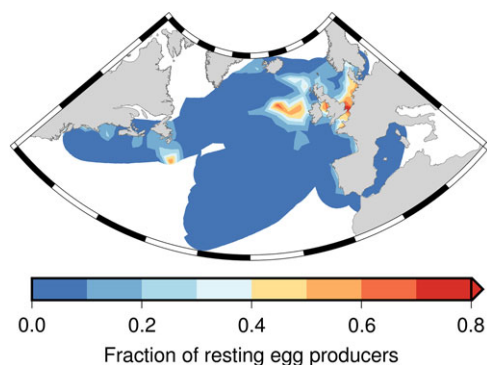


Fig. 2. Weight fraction of species producing resting eggs of the copepod assemblage in the North Atlantic. Estimates are based on CPR observations. No fractions were estimated for areas with CPR observations missing within a radius of 400 km (shown in white).

Centropages furcatus, Dana 1849 (Marcus, 1989), *Labidocera trispinosa* Esterly, 1905 (Uye, 1985), *Acartia (Acanthacartia) tsuensis* Ito, 1956 (Uye, 1985), *Calanopia americana* Dahl F., 1894 (Marcus, 1996), as they are only referred to in the literature as “unpublished data”. Secondly, some species

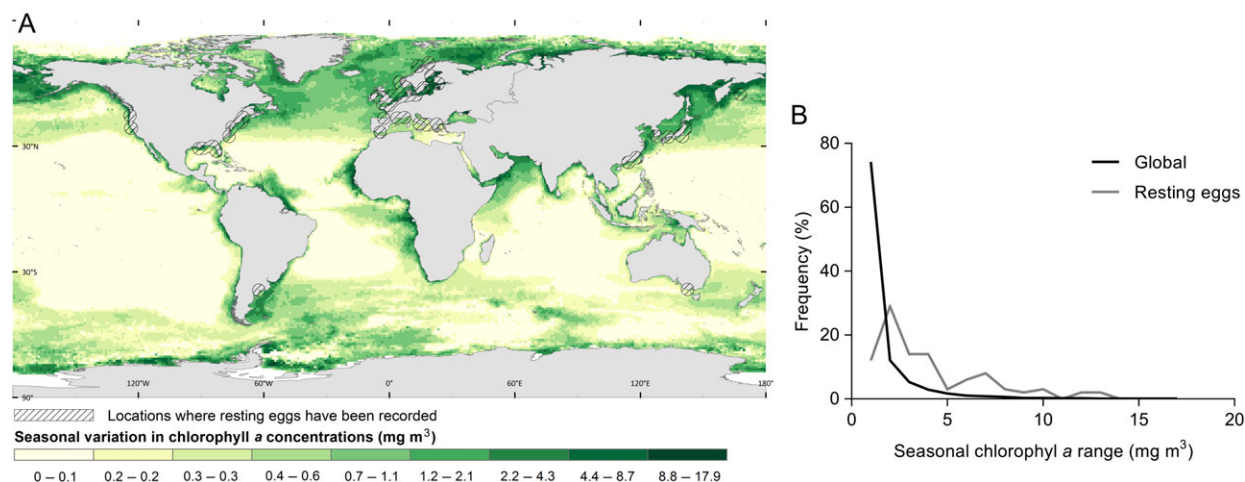


Fig. 3. (A) Locations where resting eggs for marine free living calanoid copepods have been recorded (hatched areas) and the global pattern in seasonal variation in chlorophyll *a* concentrations (difference between monthly maximum and minimum concentrations, mg m^{-3}). (B) Global frequency distributions of the seasonal variation in chlorophyll *a* concentration and the frequency distribution for the areas where copepod resting eggs have been found.

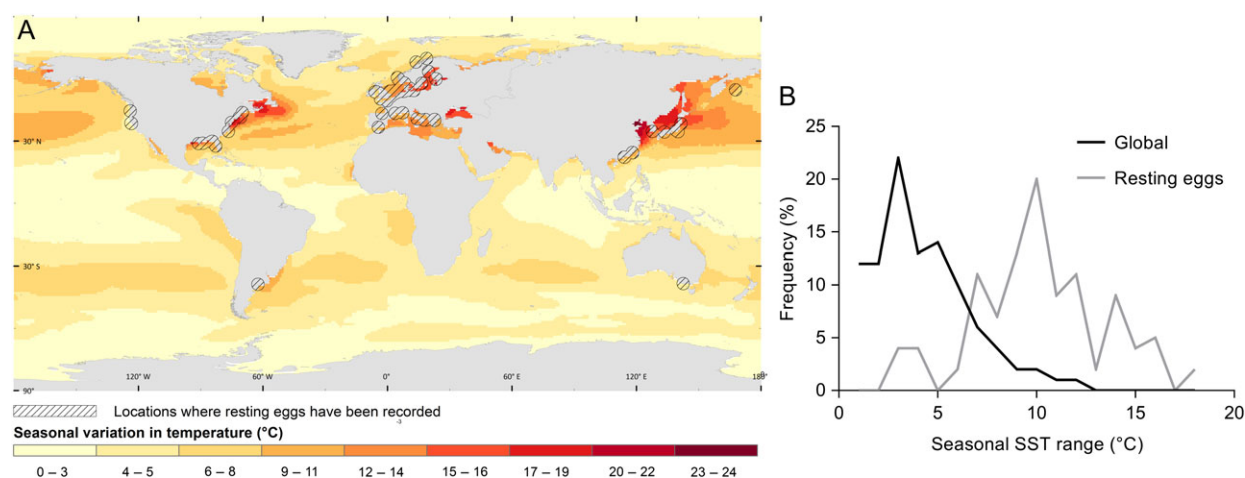


Fig. 4. (A) Seasonal variation in sea surface temperature (SST) calculated as the difference between maximum and minimum temperatures, based on long term monthly means (1981–2010). The hatched areas are where copepod resting eggs have been found (3° buffer around localities). (B) Frequency distribution of the seasonal variation in sea surface temperature and for the areas where copepod resting eggs have been reported ($\theta = 1.6$ decimal degrees around).

have been reported twice due to changes to the species name, viz. *Labidocera rotunda* (synonym *Labidocera bipinnata*) and *Centropages tenuiremis* Thompson and Scott, 1903 (*Centropages yamadai*) (Uye, 1985). Furthermore, species such as *Centropages typicus*, *Acartia* (*Acartiura*) *longiremis* Lilljeborg, 1853 and *Acartia* (*Acanthacartia*) *sinjiensis* Mori, 1940, as opposed to previous indication by Mauchline (1998), have been considered as not producing resting eggs, following evidence reported by several authors (Uye, 1985; Smith and Lane, 1987; Marcus, 1990; Engel and Hirche, 2004; Durbin and Kane, 2007; Wesche et al., 2007).

Resting eggs as a life history strategy

The production of resting eggs provides a means to cope with unfavourable environmental periods (predictable and unpredictable), storing high productivity of good periods (egg bank), and to reduce genetic drift (Hairston and De Stasio, 1988). If seasonal changes in environmental conditions, affecting food uptake and survival, are predictable, then evolution would favour traits that enable organisms to cope with this seasonality (Hairston and Bohonak, 1998). However, there is significant individual variation in the production of resting

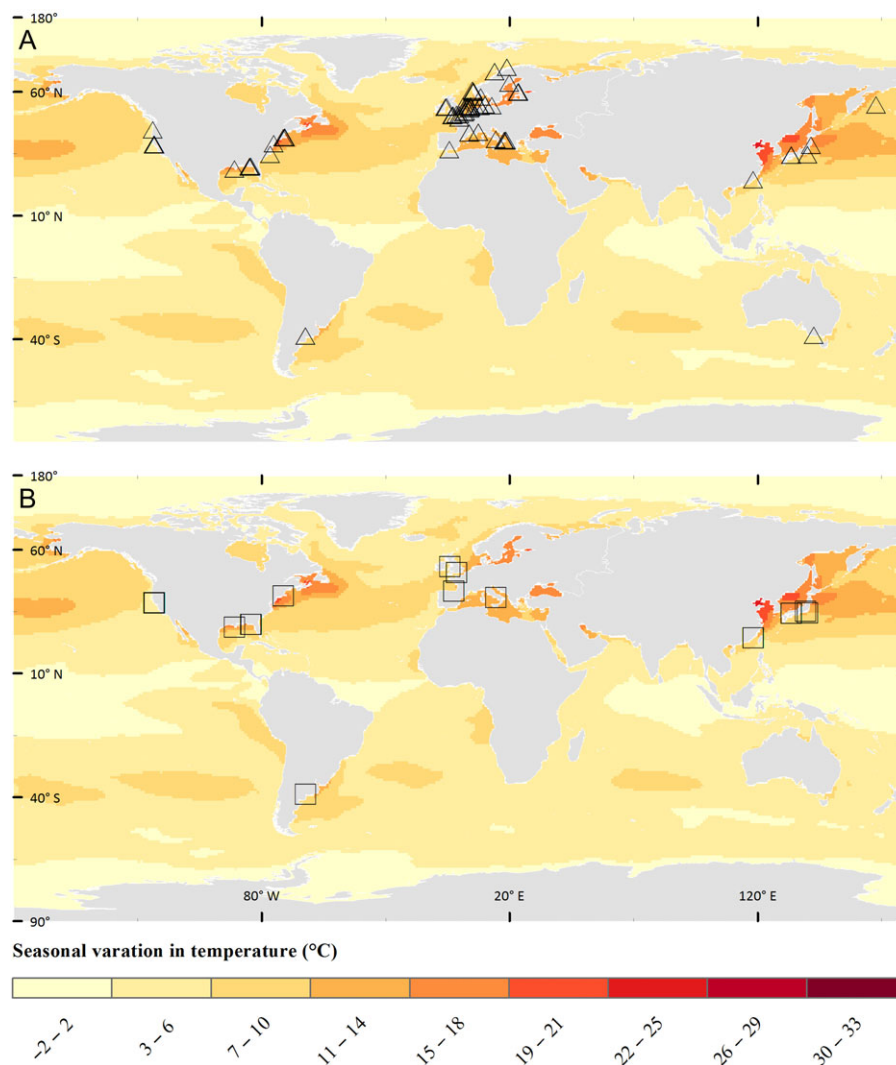


Fig. 5. Location where copepod resting eggs are produced to cope with (A) cold periods Δ and (B) warm periods □. The sea surface temperature range is calculated as the differences between T_{\max} and T_{\min} based on monthly averages covering the period 1981–2010.

eggs (Avery, 2005b) and in the duration of the refractory period (i.e. period where the egg cannot hatch) (Chen and Marcus, 1997; Engel and Hirche, 2004). If the variations in environmental conditions are unpredictable then it is expected that a strategy such as bet-hedging will evolve (Slatkin, 1974). Resting eggs (primarily diapause eggs) can function as a bet-hedging strategy by having an extended period of hatching, thus reducing the temporal variance in fitness at the expense of the arithmetic mean (Olofsson *et al.*, 2009). Hence, it might be an adaptation to the unpredictable nature of the neritic habitat, which is where resting eggs are mostly found (Fig. 1). Other resting eggs (quiescent) are a direct response to adverse environmental conditions experienced by the embryo and therefore functions as an immediate escape from adverse conditions. Therefore,

the different types of resting eggs represent different adaptations to predictable and unpredictable environmental variability, and hence function at different time scales.

Resting eggs produced on a global scale and across many copepod species may not all show a seasonal signal, as implicitly assumed in our analysis. For example, the production of resting eggs by *A. tonsa* was clearly not restricted to the thermal boundaries of its distribution, and thus the production of resting eggs is possibly also induced by non-seasonal signals. However, the overarching pattern is that resting eggs are more common in areas with a large seasonal variation in temperature (Fig. 4A and B) and, hence, mainly represent an adaptation to seasonality. We observe that resting eggs to cope with either cold or warm conditions are found towards

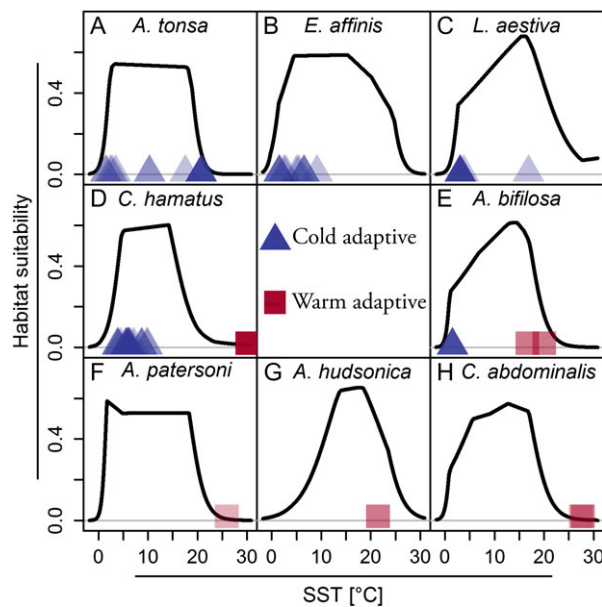


Fig. 6. Thermal niches and temperatures at resting egg locations for eight copepod species. Triangles and squares indicate the maximum and minimum monthly mean temperature at locations with cold and warm adaptive resting eggs, respectively. The intensity of the colour is an indication of the number of observations at locations with that temperature. n_p is the number of observations of the copepod species and n_{re} number of registrations of areas with resting eggs. (A) *Acartia (Acanthacartia) tonsa*, $n_p = 2336$, $n_{re} = 28$; (B) *Eurytemora affinis*, $n_p = 4594$, $n_{re} = 15$; (C) *Labidocera aestiva*, $n_p = 853$, $n_{re} = 12$; (D) *Centropages hamatus*, $n_p = 34\,719$, $n_{re} = 51$; (E) *Acartia bifilosa*, $n_p = 8156$, $n_{re} = 10$; (F) *Anomalocera patersoni*, $n_p = 2228$, $n_{re} = 1$; (G) *Acartia hudsonica*, $n_p = 458$, $n_{re} = 8$; (H) *Centropages abdominalis*, $n_p = 2266$, $n_{re} = 3$.

upper and lower thermal boundaries of the species distribution (Fig. 6). Avery (2005a) found that the cold water species *Acartia hudsonica* produce resting eggs to cope with warm conditions in Rhode Island, USA, where summer temperatures seem to exceed the lethal limit, for this species. In this area *A. hudsonica* produce resting eggs, which need a period of warming before they hatch, and therefore clearly is an adaption to the seasonal variation in temperature. However, a northern population in Maine, USA, where summer temperature is lower or in the same range, but for a shorter period, the species shows activity all year. This observation supports the idea that resting eggs are produced towards the thermal boundaries of the species distribution, because of the thermal tolerance of the species.

Resting eggs are not an overwintering strategy in the Arctic

It is striking that there are no reports of resting eggs from marine free living copepod species at high latitudes. These regions have a low seasonal variation in temperature, but large seasonal fluctuations in

availability of food, which is driven by a long winter and a short productive season (Figs 3 and 4). While this of course may be due to lack of sampling, it is consistent with observations for freshwater copepods, where egg density and the abundance of emerging nauplii from the sediment peaks at mid latitude ($\sim 54^\circ\text{N}$) and declines towards higher latitudes ($\sim 64^\circ\text{N}$) (Jones and Gilbert, 2016). Because of the short growth season and low temperature, resting eggs in the sediment may not be able to hatch, grow to maturation, and reproduce within one season. Thus, for marine copepods at high latitudes dormancy at later life stages may be more favourable. In fact, in the Arctic region overwintering as late copepodite stages and surviving the winter on accumulated lipids appears to be the main overwintering strategy (Conover and Huntley, 1991; Falk-Petersen et al., 2009; Maps et al., 2014), exemplified by the *Calanus* spp. sibling complex in the Arctic (Dahms, 1995; Hirche, 1996; Mauchline, 1998). This allows reproduction at the immediate onset of the productive period, growth and accumulation of lipids within the productive season, and supports a 1- or 2-year life cycle for *Calanus glacialis* and a 3–5-year life cycle for *Calanus hyperboreus* (Slagstad and Tande, 1990; Conover and Huntley, 1991; Hirche, 1997). Species producing resting eggs, on the other hand, typically have short lifespans and multiple generations per year (Katona, 1970; Fryd et al., 1991; Liang et al., 1996; Yoon et al., 1998; Kiørboe et al., 2015).

Factors influencing resting eggs

It remains controversial whether resting egg production is an adaptation to periods of low food, unfavourable temperatures, both, or something else. Laboratory experiments have demonstrated that resting egg production can be induced by both food and temperature, as well as by photoperiod, abrupt salinity changes, crowding and oxygen deficiency (Uye et al., 1979; Sullivan and McManus, 1986; Ban and Minoda, 1994; Chinnery and Williams, 2003; Holmstrup et al., 2006; Holste and Peck, 2006; Drillet et al., 2011). It has also been suggested that the higher protein content of resting eggs from *A. tonsa* produced under starvation is an indication of resting eggs being an adaption to cope with low food availability (Acheampong et al., 2011). In the present study resting eggs are viewed as an adaption to seasonality, which is why seasonal range and not actual values of chlorophyll *a* concentrations or SST is related to their production. We find that resting eggs are most commonly found in areas where the seasonal differences in chlorophyll *a* concentrations are significantly higher than the global average. The seasonal range in chlorophyll *a* concentrations might be affected by the ability of

zooplankton to graze down a significant fraction of the production (Schmoker *et al.*, 2013). This would dampen the seasonal difference in chlorophyll *a* concentrations, and hence the actual seasonality of the area, in terms of food availability, is not possible to detect. However, very few studies have shown food availability to be the driver or cue for production of resting eggs for both freshwater and marine copepods (Gyllström and Hansson, 2004; Drillet *et al.*, 2011). The frequency distribution from areas where resting eggs have been found, follow the pattern of the global frequency distribution, meaning that resting eggs are more often found in areas with a common range in chlorophyll *a* concentrations. The global distribution of the copepod resting egg strategy shows a stronger relationship to the seasonal variation in temperature than to the variation in chlorophyll *a* concentrations. The largest seasonal variation in temperature occurs in temperate regions on the northern hemisphere, while temperatures in the tropics and polar regions vary much less. Especially the Southern Ocean has, due to its large volume, a small seasonal variation in temperature, consistent with the observations that resting eggs are primarily found in the northern hemisphere. The notion that resting eggs are produced in areas with large seasonal differences in SST is further supported by resting eggs being produced at the boundaries of the thermal distribution of species. In contrast, seasonality in food availability is largest at high latitudes, but the productive season may be too short for resting eggs to be a viable strategy, cf. above. These differences between laboratory reports on the multiple factors inducing resting egg production and the global spatial distribution of the strategy may not be inconsistent with one another. Relating the presence of resting eggs to seasonality of temperature is done to examine the driver, not the cues for their production.

CONCLUSION

There is no clear global pattern of where copepods produce resting eggs to cope with warm or cold periods, as areas where resting eggs are produced to cope with warm conditions overlap with the areas where they are produced to cope with cold conditions. However, for several of the studied species there is a pattern showing that resting eggs are produced at the lower and higher end of their thermal distribution, despite the multiple purposes (including non-seasonal) resting eggs can have. In spite of this potential driver for the production of resting eggs, they are generally found in areas with a large seasonal variation in temperature.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

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